ANNUAL ADDRESS BY THE PRESIDENT,

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MALACOLOGY *versus* PALÆOCONCHOLOGY.

Ladies and Gentlemen,—

By long custom an annual address usually assumes the form of a summary of some sort, and most frequently that of a review of the status of the object for the advancement of which the Society addressed exists, or of some particular branch thereof.

In this wise I ventured last year to put before you some ideas concerning what evidences there might be of evolutionary processes among the Mollusca, and to-night would invite your attention to what may be called the case of Malacology *versus* Palæoconchology.

This title rather emphasizes a condition of affairs that certainly ought not to exist, but which, unhappily, does exist even yet, namely, that the gulf between the students of the recent and of the fossil forms of Mollusca is still far wider than of right it should be. Each goes too much his own way without taking account of the work of his fellow, at the same time complaining, and often with justice, that the other pays no heed to his discoveries or conclusions.

Surely it is not asking too much of the morphologist that, though apparently endowed with a plethora of recent material to work on, he should nevertheless check the results of his investigations as to the phylogenetic relationships of the groups with which he may be dealing by the corresponding work of his palæontological brethren so far as they will serve him.

On the other hand, no condemnation is too strong for the palæontologist who wilfully ignores the teaching of the morphologist and persists in classing together convergence forms, well-known at the present day (e.g. *Dreissensia* and *Septifer*), that have no natural relationship. Such only do harm to the Science by retarding its progress, and it must be regretfully added that in this they are only too frequently assisted by some students of recent forms, who occupy themselves exclusively in compiling faunal lists on antiquated lines.

Despite these dissonances among its devotees it is satisfactory to realize that some very substantial progress has been made in the study of Malacology as a whole, that becomes apparent when to the morphologist's conclusions as to the phylogeny of the phylum the touchstone of the geological record is applied.

For this purpose let us take the most recent classification of the main groups of the Mollusca from the morphological point of view, that of Dr. Paul Pelseneer in the fifth volume of the "Treatise on Zoology, edited by Sir E. Ray Lankester" (*41*). If from this, which seems to be the system most widely recognized at the present day,

we reconstruct a phylogenetic tree, taking as our basis the one by the same author in Blanchard's "Traité de Zoologie," fasc. xvi (*38*, p. 176), but correcting it to his later views and inserting, for reasons hereafter to be explained, the additional group-names "Prostreptoneura" and "Conularida," the following diagrammatic scheme results:—

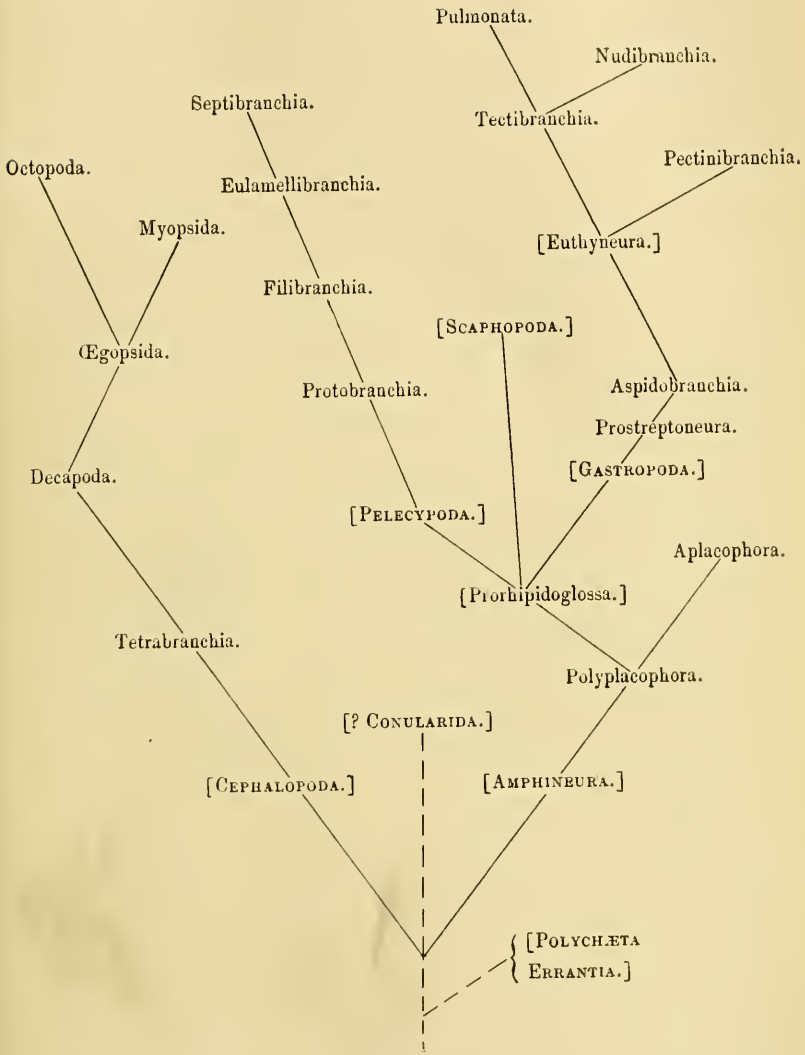

TABLE I.

It is true that phylogenetic trees, those "intellectual weeds" as Professor Sollas once wittily dubbed them, are rather out of fashion. Still, they serve a very useful purpose, bringing before the mind by the agency of the eye, more rapidly than whole pages of text can do, the opinion of the moment on the interrelationships of the members of the groups they deal with.

Next let us take the scheme thus set forth and apply it to the geological record after the manner shown in the succeeding diagram and examine the result. In this diagram the spaces allotted to the several geological formations approximate their relative thicknesses, and consequently to some extent, also, show their relative periods of duration.

Beginning with the highest molluscan group—the Cephalopoda—we find that the most archaic forms, the Tetrabranchia, of which *Nautilus* is alone the living representative, are met with as early as the Upper Cambrian, testified by seven species belonging to the genera *Orthoceras*, *Endoceras*, *Biloceras*, *Actinoceras* (?), and *Cyrtoceras* (*17*, pt. i). Continuing up into the Ordovician, the lower beds yield a transitional form, *Bactrites* (*17*, pt. iii), which, passing up to the Carboniferous, connects on through the Devonian Goniatites (*Clymenia*, etc.) with the Ammonites that flourished in the Jurassic and died out in the Cretaceous.

A long interval elapsed between the appearance of the Tetrabranchs and the arrival of the Dibranchs. From the Lower Muschelkalk (Middle Trias) near Sondershausen, Picard (*43*, p. 308) describes a form, *Campylosepia triassica*, which he considers to be an important transitional link between the Belemnites and the Sepias. Mr. Crick, however, with characteristic caution, is not prepared, owing to the obscure condition of the fossil, to endorse this opinion. At any rate, we have here a forerunner of the Decapods, of which the more primitive branch, the Œgopsida, are definitely represented in the Upper Trias by *Atractites* and *Aulacoceras*, and the higher, Myopsida, in the succeeding Jurassic by *Geoteuthis*, *Beloteuthis*, and *Teuthopsis*. The highest cephalopod group of all, the Octopoda, made their appearance in the Upper Cretaceous, with the oldest and only known fossil example, *Palæoctopus Newboldi*, H. Woodward (*58*).

So far, then, as the Cephalopoda are concerned the order of their appearance in geological time corresponds almost exactly with the phylogenetic scheme.

An interesting fossil group, the Conularida, may be taken next if only because a cephalopod affinity has been claimed for it. At one time they were relegated to the Pteropoda, and Barrande (*1*, p. 134), Matthew (*30*, p. 104), and others even identified certain lower Palæozoic forms with the existing genera *Styliola* and *Creseis*. The discovery of the morphologists, however, that the Pteropoda were in reality highly developed and specialized Opisthobranchs has in this instance been taken to heart by their palæontological confrères, and it is now generally recognized that Pteropods are not met with in earlier rocks than those of the Tertiary period.

The latest monographer of the Conularida, Miss Ida L. Slater (*47*),

considers, for reasons which in themselves are not very convincing, that *Conularia* is a mollusc appearing to resemble the primitive Cephalopoda more than any other forms, but she prefers "to regard *Conularia* as a member of an extinct group equivalent to the Cephalopods, and derived with them from the same simple shelled ancestor." As such, then, we leave them in our tables.

The Pelecypoda were yet earlier in their advent than the Cephalopoda. Two forms have been recorded from the Cambrian. The one, however, *Fordilla* of Barrande, is suspect and may be the remains of a Pod-Shrimp. The other, *Modioloides priscus*, Walcott, founded on an oval, internal cast 2 mm. long, exhibiting an anterior adductor scar and apparently a simple pallial line, is considered to be an early Protobranch.

From British Upper Cambrian (Tremadoc beds) come some obscure casts, which have been referred to several primitive genera—one doubtfully to *Orthonota*, which is also a Protobranch, others to *Palæarca* and *Glyptarca*, genera now sunk in *Cyrtodonta*. The exact position of this latter genus is uncertain; though usually placed with the Arcacea, its members, with their mixture of hinge-characters, may rather be regarded as linking the Protobranchs with the Filibranchs. Associated with these are some mytiloid shells and two pterinoid examples from an unknown horizon (*26*, p. 200; Brit. Mus. Registered No. 48762 and No. I. 2612), that may belong to *Ambonychia* or *Byssonychia*, in which case they would form some of the earliest representatives of the Pectinacea, as defined by Pelseneer, and usher in the Filibranchs, of which suborder more unmistakable examples are met with in the succeeding Ordovician period. Obviously these ancient bivalves require to be carefully re-studied in the light of the researches of the late Félix Bernard (*2*), whose premature demise was a most serious loss to Malacology.

Of the next order, the Eulamellibranchia, no representatives appear earlier than the Silurian, where a form doubtfully referred to *Lucina* (Submytilacea) has been detected, as well as one of the more highly specialized Anatinacea, *Rhytimya*. The Ostracea, represented by *Palæopinna*, only came in with the Devonian, in which, too, the first fresh-water shell, *Archanodon*, is found, its record for the Lower Devonian falling to the credit of our member, Mr. R. Bullen Newton (*32*). An early example of the Myacea, *Palæosolen*, likewise is found in beds of this age.

Of the most specialized order of the Pelecypoda, the Septibranchia, no example is met with at least till Jurassic times, if *Corburella* be admitted to this group, or with certainty till the Cretaceous, where *Liopistha* makes it appearance, followed by *Poromya* in the Tertiary.

On the whole, therefore, due allowance being made for the poverty of the early materials, the Pelecypoda fairly conform in their geological history to the conclusions based on the study of their morphology.

The Scaphopoda, having been derived, according to Pelseneer, from the same stock as the Pelecypoda and Gastropoda, might have been expected to share an equally early advent. It is true that one fossil

has been referred to this class from as far back as the Upper Cambrian, viz. *Spirodentalium osceola*, Walcott, but Pilsbry and Sharp consider this spurious and "radically unlike any form known to belong to the Scaphopoda" (*46*, p. 247). The Silurian records equally fall under suspicion, the tubes of the serpulid *Ditrupa* having frequently been mistaken for *Dentalium*. It is not, therefore, till the Devonian is reached that an undoubted member of the group is met with.

Turning next to the big class Gastropoda, we find them foreshadowed near the beginning of the Cambrian period by *Scenella* (a patelliform shell referred by common consent to the Docoglossa), by *Rhaphistoma* (one of the Pleurotomariidæ), and by two capuloid forms, *Stenotheca* and *Platyceras*, generally placed in the Capulidæ. These are reinforced in the Upper Cambrian by further representatives of the Rhipidoglossa, viz., *Murchisonia* (Pleurotomariidæ), *Cyrtolites* and *Owenella* (Bellerophontidæ), *Straparollina* (Euomphalidæ), and *Trochonema* (the type of its family), and by the curious *Subulites*, which is generally referred to the Tænioglossa.

A certain amount of complexity attends the relationships of these early Gastropods, as might be expected. Some of them are generalized types: thus the Trochonematidæ are considered by Ulrich (*52*, p. 1043) to be connected through *Trochonema* with the Pleurotomariidæ and through *Cyclonema* with the Turbinidæ.

The most difficult ones to deal with, however, are those that have been considered to belong to the Tænioglossa. To begin with, such very diverse forms have been placed together under one generic name, especially by the earlier palæontologists. As Ulrich remarks (*52*, p. 1068) of *Platyceras*, it "includes a host of wonderfully diverse shells"; and of *Holopea*, which appears in the Ordovician, he says it "embraces much that does not belong . . . [and] most diverse affinities are indicated by different sets of species, some evidently being true Littorinidæ, others related to *Cyclonema*, another set to *Platystoma*" (*52*, p. 1064).

Platyceras, as originally defined by its founder, Conrad (*7*, p. 205), contained both capuloid shells and those of a naticoid type; and though about two years later Conrad established *Platystoma* to receive these last, the name was for a long time ignored, and any shell or cast of a capuloid or naticoid character, with small spire, coming from these old beds, was forthwith put down as *Platyceras*. The name consequently carries no weight with it. Moreover, it has been rather overlooked in the past that, as pointed out in my last address (*56*, p. 248), conical shells may occur in widely different groups as a response to environmental conditions: they are none of them primitive forms of shell, but all the result of specialization to a common end—the resistance of destructive forces.

Reflecting on this and the fact that all these forms, including the Limpets, began life with a coiled, nautiloid shell, it occurred to me that the loosely-coiled forms of *Platyceras* might really represent survivors of the ancestors of the Docoglossa, and of such Rhipidoglossa as the Stomatiidæ and Delphinulidæ.

Possibly this idea may have been more or less a case of unconscious

cerebration, for, wishful to enquire further into the evolution of the Docoglossa, I re-consulted the interesting paper by Dr. Fleure (*16*),[1] and found, what had escaped my memory, the germ of the idea there.

Dr. Fleure hypothecates a prostreptoneure ancestor for the Prosobranchia, and reconstructs and figures such an animal. This prostreptoneure was in his opinion probably far more symmetrical externally than many of its descendants, with a symmetrical pair of shell-muscles, and nearly, but not quite, symmetrical shell possessing a moderately developed spiral, coiling in or near the sagittal plane, while in its anterior edge there was a sinus or slit. It had also a moderately developed operculum. Among other points in support of his contention, Dr. Fleure directs attention to the fact that "among the earliest Gastropod fossils we find many feebly spiral shells which are almost or quite symmetrical" (*16*, p. 270).

Personally I would accept Dr. Fleure's Prostreptoneura, and have, therefore, included the name in the tables, but I would define the animal and shell as perfectly symmetrical, coiling in the sagittal plane, with a complete operculum, and regard the loosely-coiled, capuloid shells found in early strata and usually referred to *Platyceras* as their modified descendants. Nor do I think the presence of the slit necessary, for, as Ulrich points out (*52*, p. 948), there is an almost total absence of a long, parallel-edged slit in the lower Silurian Pleurotomariidæ, while according to Hall, who also is not speaking of the oldest forms (*20*, p. 16), there is in many species of *Platyceras* a sinuosity of the striæ indicating a notch in the margin of the aperture during the first stages of growth, which does not always persist in the adult stage. In those in which this notch becomes closed another begins at some other point, while in others the peristome becomes plicated with several sinuosities in the mature condition. Seeing that in life most of the genus attached themselves to foreign bodies, these various sinuosities were probably due to irregularities on the surface of the object of attachment, and do not reflect any important anatomical structure in the animal.

Unfortunately the casts of these fossils do not so far appear to have yielded traces of the muscular attachment, and it is therefore not possible to say whether two distinct scars exist, or the single horseshoe-shaped scar of the Capulidæ. Koken describes and figures (*24*, p. 464, pl. xi, fig. 9) a cast under the name of *Platyceras Protei*, Œhl., from the Lower Devonian, showing the capuloid muscle-mark, but this cast obviously appertained to a shell without any spire and came from a far higher horizon than those of which we are speaking. Moreover, once the spire disappears, the strengthening of the muscle follows as a matter of course, just as in the Limpets, which equally have a horseshoe-shaped muscle attachment, but are not on that account

[1] The author desires me to mention in citing this paper that the impression accidentally conveyed here and there in it that he included certain of the Rhipidoglossa among the Docoglossa is due to an unfortunate oversight when passing the proofs, as the context of the whole paper shows.

considered allies of the Capulidæ. The horseshoe-shaped form of scar is a secondary character and not a criterion of affinity, as paired scars would be.

Pilsbry remarks of *Platyceras* that "the fusion of this genus with *Capulus* . . . is hardly justifiable" (*61*, p. 461).

Under these circumstances I would advocate the removal of these early forms from the Capulidæ and their relegation to the Prostreptoneura, the primitive stock whence both the Docoglossa and the Rhipidoglossa were derived.

Still more difficult is the case of *Subulites*. No palæontologist seems quite to know what to do with this genus. Zittel (*59* and *60*) puts them with a somewhat miscellaneous assemblage in the Pyramidellidæ and next before the Melaniidæ in his Ctenobranchia. Lindström (*28*, p. 192) created the family Subulitidæ for *Subulites* and *Euchrysalis*, to which also he considered *Bulimorpha* and *Fusispira* probably belonged. Fischer (*14*, p. 770) forms them into a family (with *Fusispira* and *Euchrysalis*) near the end of the Tænioglossa, but adds that they ought to be placed after the Strombidæ, which with him come early in the same section. Tryon (*51*, p. 246) includes them in Eulimidæ. Pilsbry (in Zittel, *61*, p. 457) retains them in Pyramidellidæ, putting that family as Fischer does in the Gymnoglossa, but at the same time admits that they "probably form a separate family." Ulrich (*52*, p. 1069) keeps them in a separate family; he retains *Subulites* for the long, slender, terebelliform species, and wisely creates a new genus, *Cyrtospira* (p. 1073), for the short, curved forms; he further associates with these *Fusispira* (p. 1075) for the more tumid forms. Finally, Pelseneer (*41*, p. 154) makes the Subulitidæ the 25th of his 55 families of Tænioglossa (in which the Gymnoglossa are included), placing them between the Melaniidæ and Nerineidæ, the Pyramidellidæ being his 53rd family.

Lindström's summing up of this question of the Subulitidæ is probably the one that will most appeal to all. He says (*28*, pp. 192, 193): "What characterizes them all, besides the elongate and smooth shells and the narrow aperture with incomplete peristome, is the important feature of a distinct apertural canal, situated exactly as in all Siphonostomata and quite as much developed as in several of them . . . We see consequently in this family the most ancient representatives of the great section of the siphonostomous shells. The systematic place of the species of this family is by far not as easily cleared up as their nature of siphonostomous shells, and I think that this question must for the present be left undecided."

Nevertheless, the consensus of opinion appears to be that the Subulitidæ belong to a higher order of Gastropoda than the Aspidobranchs, in which case it would seem that three out of the four principal divisions of the Streptoneura are first met with almost simultaneously in the oldest known fossiliferous rocks.

The fifth division, the Stenoglossa, comprising the more highly differentiated genera from *Turbinella* to *Conus*, made its appearance geologically much later, a form ascribed to *Fusus* being the first to be met with, in beds of Cretaceous age. The Jurassic *Purpuroidea*,

although included by Fischer in his Muricidæ, is more appropriately placed in the Tænioglossa.

Of the Euthyneura the Tectibranchs are the senior branch, and according to Pelseneer (*39*, p. 77) the most archaic families of the group are the Bullidæ and Acteonidæ, which are nearest in their affinities to the rhipidoglossate Trochids. Hence one would expect to meet with them early in the geological series. As a matter of fact the earliest representative that so far has been discovered appears to be a species of *Cylindrobullina* (*Scalites carbonarius*, De Kon.) in the Carboniferous.[1] This, as presently to be seen, is antedated by the Pulmonates in the Upper Devonian.

The Nudibranchs, by some lucky chance, like that which revealed *Palæoctopus*, may yet furnish a genuine glimpse of their past history. At present we fear that category will not include the exhibition before the Geological Society of Glasgow by a Mr. John Smith of "specimens of a curious set of small bodies found in a fossiliferous shale exposed on the railway from Giffen to Kilburnie in Ayrshire. These bodies are still undetermined, but belonged, he believed, to one of the Carboniferous Nudibranchs, and for which he therefore proposed the provisional name of *Archæodoris carbonarius*" (*48*).

The records of the Pulmonata in the remoter past are few but highly interesting, and since, by a strange oversight, they have not been done justice to in any single geological or other textbook, perhaps it may be well to deal with them, and some associated air-breathing Prosobranchs, a little at length.

The first discovery of Palæozoic Land Snails was made in 1852, when Sir C. Lyell, in company with Dr. (afterwards Sir) J. W. Dawson, visited the Upper Carboniferous beds at South Joggins, Nova Scotia. From the interior of an erect stump of a *Sigillaria*, they extracted some pupiform shells associated with the remains of some reptiles. These shells were alluded to and figured, but not described or named, in a joint paper in 1853 (*29*, p. 60, pl. iv, figs. 1–5). In 1858 Owen's article on "Mollusca" appeared in the "Encyclopædia Britannica" (*33*), and unaware of, or having forgotten the discovery, he states (p. 403) that "terrestrial species have not been found in strata older than the Tertiary." His attention must have been speedily called to the oversight, for in his later article on "Palæontology," which appeared in 1859 (*34*), he alludes to their occurrence (p. 111), and gives the name *Dendropupa* to them, in brackets. In 1860, when this article was reprinted as a separate work under the same title (*35*), the name is repeated (p. 79), but this time occurs in the midst of a quotation, the source of which has not yet been traced. That same year Dawson for the first time described and named the mollusc *Pupa vetusta* (*8*), but, strange to say, in his frequent succeeding references to the subject never again once alluded to this paper.

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[1] By an oversight in last year's address (*56*, p. 252), *Bullinella* from the Permian was credited with being the earliest example.

The next discovery took place in the same locality in 1866, when a small helicoid was found. This was described by P. P. Carpenter (in Dawson, *10*, p. 331: figs.) under the name of *Zonites* (*Conulus*) *priscus*. The species was subsequently referred to *Archæozonites* (Zittel, *60*, p. 365), but Pilsbry now places it in *Pyramidula* (?) (*45*, p. xxxix).

In 1869 Mr. F. H. Bradley obtained two new forms of Land Shells from the concretionary limestone accompanying the underclay of coal at Pelly's Fort, Vermilion River, Illinois (*3*, p. 254). These were described by him in 1872 (*4*, pp. 87–88) as *Pupa Vermilionensis* and *Anomphalus Meeki*. He subsequently recognized that the latter was not, as he had supposed, a marine shell, and removing it from Meek's genus, defined it as a helicoid and created the genus *Dawsonella* for its reception (*5*, p. 151).

In 1880 Sir J. W. Dawson published a "Revision of the Land Snails of the Palæozoic era" (*11*), adding to the list *Pupa Bigsbii*, from the South Joggins Coal-measures, and *Strophites grandæva*, from the still older Erian (Devonian) Plant-beds of St. John, New Brunswick.

The following year Mr. R. P. Whitfield (*55*) described and figured from the higher beds of the Coal-measures, near Marietta, Ohio, a strongly striate, toothed pupoid shell, under the name of *Anthracopupa Ohioensis*. At the same time he alluded to Bradley's *Dawsonella*, which on the evidence obtained from better material he referred to the Helicinidæ.

C. D. Walcott next, in 1883 (*53*, p. 808; and *54*, pp. 261–263), described and figured from the lower portion of the Carboniferous group, on the western slopes of New York and Richmond Mountains, Eurika district, Nevada, a remarkable elongate and obviously terrestrial form under the name of *Zaptychius carbonarius*. With it were found two fresh-water forms described as *Physa prisca* and *Ampullaria* (?) *Powelli*.

The Middle Permian beds of Chambois, Saône-et-Loire, were the next to yield a terrestrial mollusc described by Dr. P. Fischer (*15*, p. 100: fig.) as *Dendropupa Walchiarum*.

Sir J. W. Dawson, in his "Synopsis of the Air-breathing Animals of the Palæozoic in Canada up to 1894" (*12*, pp. 83–84), includes "*Pupa pervetus*, Matthew," which proves to be an intended reference to a species described in a succeeding paper by G. F. Matthew (*31*, p. 98, pl. i, figs. 10*a* and *b*) as *Pupa primæva*. Either Dawson took a wrong note when Matthew's paper was read or the name was changed on going to press. This species came from the same Upper Devonian bed that yielded the *Strophites grandæva*.

Finally Dr. Smith Woodward has just obligingly drawn my attention to some specimens sent to the Natural History Museum by Dr. I. C. White, State Geologist, of West Virginia, U.S.A., for determination. These include, besides a millipede and some ostracod remains, examples of small terrestrial Gastropods very like *Dendropupa*, and a possible helicoid. They come from the Peruvian limestones near Valley Grove, Ohio County, West Virginia.

In this little group of Palæozoic air-breathers we have the earliest terrestrial Rhipidoglossate, if we accept, as I think we may do, Whitfield's determination of *Dawsonella* as such, the oldest known *Ampullaria*, for Walcott's "?" seems unnecessary, and the first of the Pulmonates.

Both divisions of the last-named order are represented, the Basommatophora by *Physa* and *Zaptychius*. The determination of the *Physa* is probably correct, for one would hardly look for so highly differentiated a form as a sinistral *Limnæa* at so early a period in the world's history; moreover, *Physa* is the more primitive of its congeners, its radula being less specialized than those of *Limnæa* or *Planorbis*, both of which are met with far later in the record of the rocks.

Zaptychius, however, connotes an older family, since, according to Walcott—and our Editor, Mr. E. A. Smith, agrees in that opinion—it "appears to have its nearest ally in *Auricula*." Pelseneer holds (*37*, p. 114; *40*, p. 66) that the Auriculidæ are nearest akin to the Opisthobranchs and are consequently the most archaic of the Pulmonates, and present the greatest number of characters common to both Basommatophora and Stylommatophora. By right, therefore, they should make their appearance earlier in the geological sequence than the more specialized Stylommatophora. This they just fail to do, for Dawson's *Strophites*, although fragmentary, certainly seems to belong to the Pupidæ, although not identical, as he subsequently appears to have thought, with *Strophia—Cerion* as we now know it.

The remaining Pupidæ—for such they probably are, unless, like *Sphyradium*, the *Dendropupa* group belongs really to the Endodontidæ—fall into two divisions, those with and those without teeth, neither of which can it be pretended is identical with *Pupa* itself.[1] It seems, therefore, most reasonable for the present, till further material shall be forthcoming, to provisionally range the edentulous species under *Dendropupa*, and the dentigerous under *Anthracopupa*.

It may facilitate purposes of reference if the information here gathered concerning these Palæozoic Pulmonates be summarized as follows:—

HELICINIDÆ.

Dawsonella Meeki, Bradley. Upper Carboniferous.

[Mentioned, but not named] Bradley: Rept. Geol. Surv. Illinois, vol. iv (1870), p. 254.

Anomphalus Meeki, Bradley: Amer. Journ. Sci., ser. III, vol. iv (1872), p. 88, fig.

Dawsonella Meeki, Bradley: as a helicoid, op. cit., vol. vii (1874), p. 151: belongs to Helicinidæ, Whitfield, op. cit., vol. xxi (1881), p. 127, figs.

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[1] Dawson's comparisons with recent forms do not seem altogether happy ones.

AMPULLARIIDÆ.

Ampullaria Powelli, Walcott. Lower Carboniferous.

Ampullaria (?) *Powelli*, Walcott: Science, vol. ii (1883), p. 808, figs.; U.S. Geol. Surv., Monog. viii (1884), p. 261, figs.

AURICULIIDÆ.

Zaptychius carbonaria, Walcott. Lower Carboniferous.

Zaptychius carbonaria, Walcott: Science, vol. ii (1883), p. 808, fig.; U.S. Geol. Surv., Monog. viii (1884), p. 263, fig.

PHYSIDÆ.

Physa prisca, Walcott. Lower Carboniferous.

Physa prisca, Walcott: Science, vol. ii (1883), p. 808, fig.; U.S. Geol. Surv., Monog. viii (1884), p. 262, fig.

ENDODONTIDÆ.

Pyramidula (?) prisca (Carpenter). Upper Carboniferous.

Zonites (*Conulus*) *priscus*, Carpenter: in Dawson, Quart. Journ. Geol. Soc., vol. xxiii (1867), p. 331, figs.; Dawson, Amer. Journ. Sci., ser. iii, vol. xx (1880), p. 411, figs.

Archæozonites [*priscus*, Carp.], Zittel: Grundzüge der Paläontologie (Paläozoologie), Abth. i, Invertebrata, 1895, p. 365; 2nd ed. (1903), p. 393.

Pyramidula (?) [*prisca*, Carp.], Pilsbry: Man. Conch., ser. ii, vol. ix (1894), p. xxxix.

PUPIDÆ.

Strophites grandæva, Dawson. Upper Devonian.

Strophites grandæva, Dawson: Amer. Journ. Sci., ser. iii, vol. xx (1880), p. 413, fig.

Strophia (*Strophella*) *grandæva*, Dawson: Trans. Roy. Soc. Canada, vol. xii (1895), sect. iv, p. 84.

Dendropupa vetusta (Dawson). Upper Carboniferous.

Pupa [sp.], Lyell & Dawson: Quart. Journ. Geol. Soc., vol. ix (1853), p. 60, pl. iv, figs. 1–5.

Dendropupa [sp.], Owen: article "Palæontology," Encyc. Brit., 8th ed. (1859), p. 111; "Palæontology," 1860, p. 79.

Pupa vetusta, Dawson: Quart. Journ. Geol. Soc., vol. xvi (1859), p. 270, figs.; vol. xviii (1862), p. 7 (mentions in footnote Owen's name of *Dendropupa*); "Air-breathers," 1863, p. 67, pl. iv, figs. 49–53.

Pupa (*Dendropupa*) *vetusta*, Dawson: Trans. Roy. Soc. Canada, vol. xii (1895), sect. iv, p. 83.

Dendropupa Bigsbii (Dawson). Upper Carboniferous.

Pupa Bigsbii, Dawson: Amer. Journ. Sci., ser. iii, vol. xx (1880), p. 410, figs.; Trans. Roy. Soc. Canada, vol. xii (1895), sect. iv, p. 84.

DENDROPUPA WALCHIARUM, Fischer. Middle Permian.

Dendropupa Walchiarum, Fischer: Journ. de Conchyl., tom. xxxiii (1885), p. 100, fig.

DENDROPUPA PRIMÆVA (Matthew). Upper Devonian.

Pupa pervetus, Matthew; n.n. Dawson: Trans. Roy. Soc. Canada, vol. xii (1895), sect. iv, p. 84.

Pupa primæva, Matthew: loc. cit., p. 98, pl. i, figs. 10*a* and *b*.

ANTHRACOPUPA OHIOENSIS, Whitfield. Upper Carboniferous.

Anthracopupa Ohioensis, Whitfield: Amer. Journ. Sci., ser. III, vol. xxi (1881), p. 126, figs.

ANTHRACOPUPA VERMILIONENSIS (Bradley). Upper Carboniferous.

[Mentioned, but not by name] Bradley: Rept. Geol. Surv. Illinois, vol. iv (1870), p. 254.

Pupa Vermilionensis, id.: Amer. Journ. Sci., ser. III, vol. iv (1872), p. 87, fig.; Dawson, op. cit., vol. xx (1880), p. 410, figs.

The fact that a European example of a Palæozoic Land Snail has been found, albeit of a later age than the described American ones, should encourage research in this country, where doubtless, when looked for in likely situations, examples will also be found.

Another early form of Gastropod calls for mention here, and that is *Hercynella*, because by some authorities it has been placed with the Siphonariidæ on account of the curious fold running from the apex to the margin of the patelliform shell. Now Pelseneer has pointed out (*40*, p. 67) that *Siphonaria* is a Basommatophore that has secondarily become adapted to a marine life. With such an origin an example is hardly likely to be found so early in the geological sequence as the Devonian; even *Anisomyon*, from the American Cretaceous, seems doubtful, and unquestioned examples only come in with the Tertiary period. Moreover, a careful scrutiny of the most recent figures (Perner, *42*, tom. i, pls. xliv–l; tom. ii, pls. cv, cxviii–cxxiii) does not give at all the impression that *Hercynella* belongs to the Siphonariidæ; indeed, the characteristic fold partakes far more of the channel observable in *Subemarginula*, near which it has been placed by some palæontologists. Fischer (*14*, p. 861) inclines to ally it with *Capulus*, and consequently *Platyceras*. Probably it would be most correctly placed as an aberrant form of the then decadent Prostreptoneura, but further evidence is required.

The past history of the Gastropod branch of the Molluscan phylum is on the whole, therefore, less consonant with their morphological genealogy than is seen to be the case in the Cephalopoda and Pelecypoda.

There remains now the class Amphineura to consider.

These molluscs are generally held to be a very primitive group, and Pelseneer shows them to be the most archaic of recent Mollusca, and derives from them all the other classes save the Cephalopoda (*39*, pp. 1–41 and 82). Hence, to accord with their morphological position they should have been the oldest mollusc geologically. This, however, is not the case, and they are not met with in any strata older than the Ordovician, when the genus *Priscochiton* makes its appearance,

followed by *Helminthochiton*, *Chelodes*, etc., in the Silurian, *Probolæum* in the Devonian, *Gryphochiton* in the Carboniferous, and so on. For these Palæozoic Chitons Pilsbry (in Zittel, *61*, p. 434) has established the family Gryphochitonidæ, characterized by the absence of insertion plates. The modern Lepidopleuridæ, which date from Tertiary times, are closely allied to them, and, though the higher genera of this family possess insertion plates, these are still unslit. This antique type has only been able to exist to the present time by taking to deeper water, where competition in the life-struggle is less severe (Pilsbry, *44*, p. x).

That older representatives of the Polyplacophora will yet be found, I feel sure, and would suggest search for them among fossils referred to the plates of Pod-Shrimps, seeing that one at least has thence been brought to light (H. Woodward, *57*, pp. 356–358).

The more highly specialized Aplacophora have not been recorded fossil as yet, but some day an energetic microscopist, if any such be left, may when hunting over fossil sponge-spicules come on examples of those of these interesting molluscs.

Measured, then, against the record of the rocks as at present revealed to us, the story of molluscan development according to the latest morphological investigations, based on the study of living forms, is not in complete harmony therewith, although much more so than one would at first be led to suspect. The Amphineura, Scaphopoda, and Opisthobranchia all make a relatively more tardy appearance in the strata than they theoretically should do, while the early Gastropods have distinctly not sorted themselves out phylogenetically. This circumstance is due largely no doubt to the imperfections in the geological record, largely also to the fact that the true relationships of those fossil forms that are known to us, especially the older ones, are not yet satisfactorily determined. Chiefly is this the case with the Gastropoda, in which class, as Eastman remarks (*61*, p. 502, note), "the difficulty of adapting a strictly zoological classification, based upon the anatomy of the soft parts, to the practical needs of the palæontologist is strikingly illustrated."

Although this difficulty may never be entirely overcome, many of the gaps in our knowledge may be successfully bridged by steady patient work of the kind already attempted by Hyatt, Buckman, Waagen, and others, for the Ammonites; by Cossmann, Grabau, and others, for the Gastropods; and by Jackson for the Pelecypods; the method adopted being to trace out the relationship and succession of the various allied species in a given group, or, better still, to trace the morphology of a given form both laterally along a definite horizon, and vertically into successively newer and newer beds. It had been my intention to allude more fully to this method of working, and the class of results it yields, but the subject is one that will well bear treatment at greater length on some future occasion when more time can be devoted to it.

The lacunæ in our knowledge of the interrelationships of the members of the various families and orders of Mollusca are slight, however, compared with the blank caused by the total absence from

palæontological history of any hint of passage forms between the classes themselves, or between the Mollusca and their nearest allies. Nor is this hiatus confined to the Molluscan phylum; it is the same for all branches of the animal kingdom. There is circumstantial evidence that transitional forms must have existed, but of actual proof none whatever. All the classes of Mollusca appear fully fledged, as it were. No form has as yet been discovered of which it could be said that it in any way approached the hypothecated prorhipidoglossate molluse, still less one linking all the classes.[1]

Howbeit, behind the period yielding the earliest fossils known to us must have lain an age equally vast as that separating us from it, and we can only hope that in some yet geologically unexplored region of the earth's surface, examples of older rocks may be found that have escaped the metamorphic agencies which have rendered ours azoic. At present we can only dimly infer from such available material as we have what the connecting links between these forms of life may have been in the past.

Perhaps, by way of conclusion, a word or two as to the possible ancestry of the Molluscan phylum may not be out of place.

The subject has had a good deal of fascination for the morphologists, but dealing with recent material and mostly being unfamiliar with the palæontological aspect and its requirements, the conclusions they have arrived at have been rather various.

The two principal theories are (1) that the Mollusca were derived from the Flat-Worms of the Class Turbellaria, and (2) that they come from the Segmented Worms (Annulata), while recently R. T. Günther (*19*) has sought to show that the Chætognatha are the primitive Mollusca. This last hypothesis has been met by Thiele (*50*) with arguments which though brief seem effective, quite apart from the fact that it does not seem practicable to compare so highly specialized a being as a Chætognath with such equally highly differentiated Molluscan forms as the Dibranchiate Cephalopods and the Pteropoda.

The Turbellarian ancestry of the phylum has been advocated by Lang (*27*), Thiele (*49*, pp. 507–508), and others, Thiele more particularly indicating the Polycladia Cotylea (*49*, p. 529) as the stem. Korschelt and Heider admit that the theory has much to be said for it, but consider "this origin has the disadvantage of starting from very highly differentiated animals, and . . . affords no explanation of the striking resemblance existing between the larvæ of the Mollusca and those of the Annelida" (*25*, pp. 320–321). Pelseneer, however (*36*, p. 368), and Garstang (*18*, pp. 39–44) had already, as it seems to me, sufficiently disposed of the arguments urged in favour of a Polyclad ancestry, the latter postulating a common stem whence the Polyclads branched off on one side and the Annelida

[1] W. K. Brooks (*5a*) has developed a somewhat fantastic idea to the effect that the earliest animals were pelagic, that the principal groups evolved them, and that they subsequently discovered and colonized the sea-floor when they became fossilized. This leaves out of account the fact that pelagic animals drop to the bottom and become fossilized also.

and Mollusca on the other. Conklin (*6*, pp. 192 et seqq.) dwells on the remarkable similarity between the early pretrochophore stages of development in the Annelida and Mollusca. Korschelt and Heider (*25*, pp. 321–2 and 327) incline to the Annelid affinities of the Mollusca; they point to the trochophore stage (trochosphere of Lankester) in both as indicating a common ancestry, and proceed to construct a primitive mollusc therefrom. This is always a dangerous proceeding, and, as they seem to have expected themselves, subsequent discoveries have demolished much of their structure. Other points of agreement that they indicate as existing between the two phyla are—"the conditions of the cœlom," which "agree in such a striking manner . . . that it is difficult to believe that two structures so remarkably alike arose in different ways" (*25*, p. 326), the occurrence of the nephridia and their connection with the cœlom, and the great resemblance of the circulatory system of the Mollusca to that of the Annelida (p. 327).

Pelseneer is yet more explicit, and as early as 1892 (*36*, pp. 371–372) concluded that the Mollusca came nearest to the Polychæta Errantia, and more especially to *Eunice*. The resemblances on which he relies are set forth more fully in his "Mollusques Archaïques" (*39*, pp. 85–87); they include the similarity in the early development in the two classes that has already been alluded to, the structure of the eyes and organs of taste, of the spicules and the generative organs, while in addition the Eunicidæ possess a muscular pharynx, with a cæcal invagination under the œsophagus enclosing chitinous denticles, all which points are paralleled in the buccal mass, radula sac, and radula of the Mollusca. In *Staurocephalus*[1] the similarity of the chitinous denticles to radula teeth is striking. Moreover, the anterior portion of the nervous system in *Eunice* and the Mollusca is, as Pelseneer shows, wonderfully similar. He also would, therefore, derive the Annelida and the Mollusca from a common stock.

It may further be noted that, although the modern morphologist is, as a rule, as chary of mentioning it as the shell-collector is of alluding to the 'nasty animal,' not a few molluscs do possess shells, and that while the morphologist is apt to treat its occurrence as a matter of no moment and a phenomenon that might readily arise at any time, Nature does not seem to acquiesce in this opinion. For except in the case of some of the most highly specialized, shell-less, forms of all, in which by acceleration of development the stage has been suppressed, all molluscs alike start in the egg with an exogastric nautiloid shell. The shell, therefore, being an embryonic character, would point to an ancestry that possessed this feature, and it is suggestive that of all the Worms the Polychæta alone furnish examples provided with calcareous tests (*Spirorbis*, *Serpula*), although in their case there is no organic connection between the animal and its shelly tube.

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[1] What the valid name of this Worm may be is at present uncertain. *Staurocephalus* is preoccupied for Trilobita, and the synonyms, *Anisoceras* and *Prionognathus*, quoted by Carus, are equally forestalled for other branches of the Animal Kingdom.

Another apparent parallelism may be adduced, namely, the spiny girdle of some Polyplacophora and the fringe of iridescent spicules borne by the Sea-Mouse (*Aphrodite*).

The remains of Polychæta, moreover, like those of the Mollusca, date back to early Palæozoic times. The tubes of *Spirorbis* (or kindred genera) are found abundantly in the strata from the Ordovician onwards, and *Serpula* from the Silurian. More important still was the discovery by Dr. Hinde of detached jaws and toothed plates of forms of Polychæta Errantia (*Eunicites*, *Arabellites*, *Œnonites*, etc.) in Palæozoic rocks, from the Ordovician to the Carboniferous, of Canada, Great Britain, and Sweden (*21*, *22*, *23*), while they have also been found by Mr. R. Etheridge, jun., in the Upper Silurian of New South Wales (*13*).

Such, then, so far as I am able to sum it up, is the case of Malacology *versus* Palæoconchology, and I here leave it to your judgement, pausing only to cordially acknowledge the kind help I have received on certain desired points from my colleagues, Dr. A. Smith Woodward, Mr. E. A. Smith, I.S.O., Mr. Crick, Mr. Bullen Newton, and Dr. Calman, as well as from my friend Mr. Pace and others.

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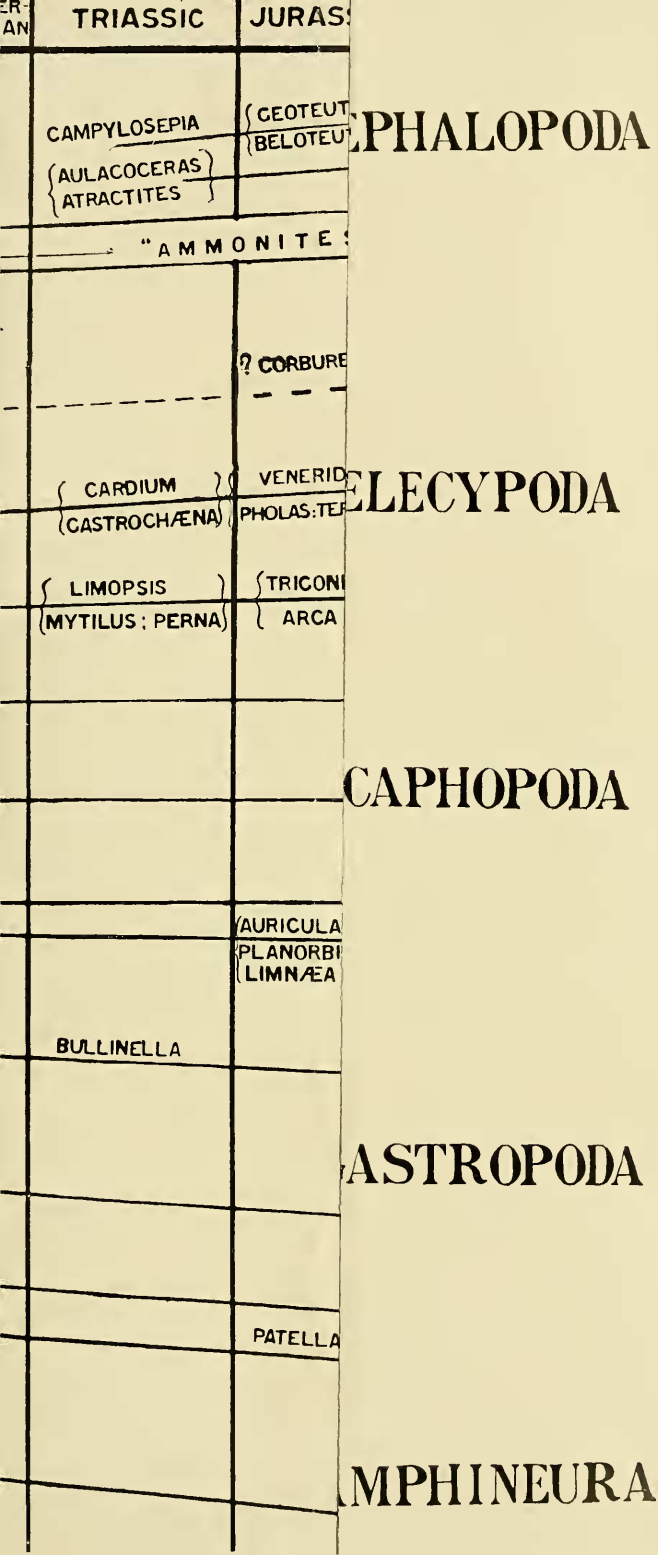
TRIASSIC
JURAS
CAMPYLOSEPIA
AULACOCERAS
ATRACTITES
GEOTEUT
BELOTEU
PHALOPODA
"AMMONITE
? CORBURE
CARDIUM
CASTROCHÆNA
VENERID
PHOLAS: TE
LECYPODA
LIMOPSIS
MYTILUS: PERNA
TRICONI
ARCA
CAPHOPODA
AURICULA
PLANORBI
LIMNÆA
BULLINELLA
ASTROPODA
PATELLA
MPHINEURA